E

Evolutionarily Stable Strategies

François-Xavier Dechaume-Moncharmont
Evolutionary Ecology Group, Université de Bourgogne Franche-Comté, UMR CNRS 6282 Biogéosciences, Dijon, France

Definitions

- *Strategy*: set of (behavioral) phenotypes or decision rules having evolved under natural selection.
- *Evolutionarily stable strategy*: strategy that, when resident (i.e., adopted by most members a population), cannot be invaded by an initially rare alternative strategy (also referred to as mutant).
- *Darwinian fitness*: expected reproductive contribution to future generations.
- Frequency dependence: dependence of the fitness payoffs of a strategy on the frequency of the other strategies in a population.

Introduction

The concept of evolutionary stable strategy (ESS) is an essential part of the behavioral ecologist's toolbox. It belongs to the general field of game theory, which is extensively used to describe and analyze the evolution and the maintenance of (behavioral) phenotypes in a population. Such formal analysis is particularly relevant due to the complex interdependence between the members of a population. The adaptive value of a behavior can rarely be assessed on its own merit irrespective of the behaviors of the individuals from the rest of the population. For instance, the efficiency of a fighting technique could depend upon its scarcity. While left-handedness does not provide intrinsic mechanical or cognitive benefits in noninteractive sports, being a rare left-handed opponent offers a strategical advantage in many sports involving direct interaction between players as in combat sports, tennis, or cricket (Llaurens et al. 2009). This could be explained by a surprise effect, their opponents being more accustomed to practicing against right-handed players. Consequently, left-handed players are overrepresented in these sports compared to their proportion in the general population. Their frequency increases until their opponents have enough opportunities to be accustomed to their playing style. The proportion of left-handed and right-handed players reaches an equilibrium characterized by the fact that no handedness is advantageous compared to the other.

Such cases of frequency dependence are ubiquitous in nature. For instance, in *Perissodus microlepis*, a small cichlid fish from Lake Tanganyika which feeds on scales of other fish, some individuals are specialized in attacking their prey from the left side, while other are specialized on the right side. The proportions of these two strategies oscillate around 50%. The rarer morph

© Springer International Publishing AG 2018
J. Vonk, T.K. Shackelford (eds.), *Encyclopedia of Animal Cognition and Behavior*,
https://doi.org/10.1007/978-3-319-47829-6_1808-2

temporarily benefits from lower vigilance by their prey which is more often attacked on the other side by the more abundant morph (Hori 1993). Frequency dependence is not restricted to discrete strategies; it is also relevant for continuous strategies such as the level of selectivity during mate choice. Even when the individuals gain direct benefits from pairing with the highest quality partners, the evolution does not necessarily lead to very selective strategies. Being picky would theoretically allow a female to find a high-quality male if she was the only chooser in the population. But if there are other females competing for the same pool of males, the female would be better accepting even a mediocre partner. A greedy female trying to outsmart her unselective competitors by increasing her choosiness exposes herself to the risk of losing the mate race, all the males being progressively removed from the pool of potential partners by less selective females while she is unsuccessfully searching for her ideal, yet no longer available, male (Dechaume-Moncharmont et al. 2016). The average partner quality that a female can expect when following a given decision rule cannot be calculated as an absolute value. It is strongly dependent upon the frequency of the other strategies in the population through the background distribution of the remaining male's quality. Searching for the optimal sampling strategy of a given individual thus requires to explicitly consider the behaviors of its competitors.

Nash Equilibrium

The kind of problems described above, with complex interdependent decision-making, belongs to the general field of game theory, which started to attract considerable attention from mathematicians and economists when von Neumann and Morgenstern's published their seminal book *Theory of Games and Economic Behavior* (1944). Among the family of game theory, one is particularly relevant in biology, the noncooperative game in which the players are not assumed a priori to cooperate or to form binding agreements. The cooperation between the players can emerge from such games as a consequence of the interaction but not as a prerequisite. The central assumption is that the players act rationally and try to maximize their payoffs. The difficulty is to find the possible outcomes from the interactions between the players. A decisive result has been formulated by John Nash (1950), which earned him the Nobel Prize in Economics in 1994. He characterized the solution of a noncooperative game as an equilibrium, which is now referred to as "Nash equilibrium." He gave a very concise definition of this concept which can be summarized as: an equilibrium point is reached when the strategy of the players cannot be strictly outperformed by another strategy. In other words, no player would be tempted to switch strategies because he would not increase his payoffs by unilaterally deviating from the equilibrium point.

Evolutionary Game Theory

A very strong assumption of the classical game theory is that each players acts rationally, which means that they purposely behave in order to maximize a criterion of self-interest. Yet, the existence of rational decision-making has been challenged many times in experimental psychology. The ecologists considered the problem from a completely different perspective than the economists or the psychologists. William Hamilton and Robert Trivers were among the first biologists to acknowledge the relevance of game theoretical framework in evolution, but the field of evolutionary game theory was founded by John Maynard Smith and George Price (1973). They introduced the concept of *evolutionarily stable strategy*, which is closely related to the Nash equilibrium. The key idea behind the concept of ESS is that the individual behaviors directly affect its Darwinian fitness, namely, its probability to survive, reproduce, and contribute to future generations. The best strategies lead to higher reproductive success, and thus, their frequency increases in the population across generations. On the contrary, the least efficient strategies are progressively washed away by the natural selection. This evolutionary perspective is an elegant way to escape the questionable assumption of perfect rationality in classic game theory, which assumes that agents are able of complex calculation to determine the appropriate action. Evolutionary game theory does not require any cognitive skills for the players. It is the natural selection itself which performs the decision-making procedure: strategies are favored provided they performed well in the environments in which they evolved. This hypothesis of *ecological rationality* is a decisive improvement because the process of natural selection is a clearly defined mechanism. The term strategy could even to be understood in a very broad sense as any set of phenotypes affecting the Darwinian fitness of the individual, as long as they are able of replication: they are heritable and can be transmitted to the next generation. Following that definition, plants, fungus, or microorganisms can perfectly adopt an ESS without any rational thinking. For instance, in bacteria, one can describe the probabilities to cooperate with neighboring cells and contribute or not to the collective defense as strategies which can be analyzed in a game theoretical framework (Frey 2010).

The concept of ESS is grounded on the existence of mutation which randomly appears in the population. In the evolutionary biology jargon, a mutant is any alternative strategy challenging the resident strategy and trying to invade the population. A strategy is said to invade if, when rare, it does better than the prevailing strategy and so spreads in the population and become the new resident strategy. An ESS is characterized by its stability, i.e., its ability to resist the invasion by a mutant. This property can be formulated in mathematical terms (Maynard Smith, 1982). Write $W(p, q)$ the fitness of a player following the strategy p in a population of players following the strategy q. If p is the ESS, no rare mutant strategy q can outcompete p when it is resident in the population:

$$W(p,p) \geq W(q,p), \text{for all}\, q. \qquad (1)$$

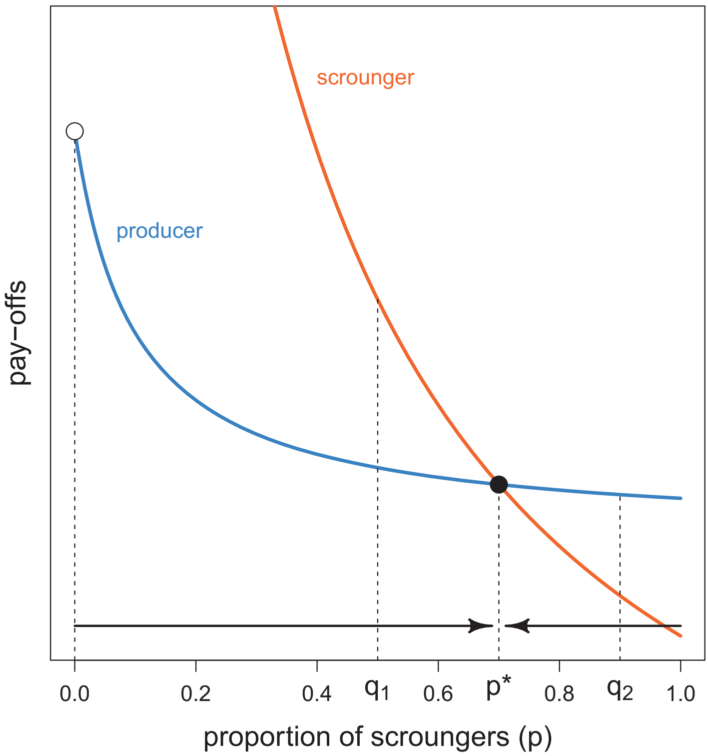
This first condition corresponds to the Nash equilibrium. It is, however, possible that the rare mutant strategy q does as well as the resident strategy: $W(p, p) = W(q, p)$. While it is not strictly favored by natural selection, the frequency of the mutant may increase by the neutral process of genetic drift. In other words, the average resident strategy in the population is likely to change. In such case, the Nash equilibrium condition verifying that the strategy p cannot be outperformed (Eq. 1) is not sufficient. To ensure its evolutionary stability, the ESS should also be able to invade other strategies:

$$\begin{aligned} &\text{if}\ W(p,p) = W(q,p), \\ &W(p,q) > W(q,q), \text{for all}\, q \neq p. \end{aligned} \qquad (2)$$

The only best response to an ESS is the ESS itself. Note also that the concept of ESS is more restrictive than the Nash equilibrium: every ESS is a Nash equilibrium, but all Nash equilibrium is not necessarily an ESS.

Evolutionary Stable Strategy and Population Optimality

The concept of ESS has an important heuristic value in biology because it is a powerful argument against group selection as a major mechanism for the evolution of cooperation: most collectively optimal strategies are very fragile and highly unstable when confronted to selfish mutant strategies. To illustrate this point, one can consider the classical example of the producer-scrounger game (Giraldeau and Caraco 2000). In many species, the foraging strategy of the individuals can be categorized in two contrasted behaviors: the producers actively search for food on their own, while the scroungers try to steal a portion of the food discovered by the producers. Consider a population with proportion p of scroungers, and $1 - p$ of producers. The producers are bearing all the costs of active food searching. A scrounger takes advantage of the active food searching of the producers and thus negatively affects its foraging efficiency. The total amount of food per individual, which can be used as a proxy of the fitness payoffs, decreases as the proportion of scroungers



Evolutionarily Stable Strategies, Fig. 1 The fitness payoffs of the producers and scroungers are frequency-dependent: they both decrease with p the proportion of scroungers in the population. The plot should be read vertically: a given state of the population corresponds to a given proportion of scroungers, which allows comparison on both fitness payoffs. For any proportion of scroungers $q_1 < p^*$, the scroungers have higher fitness payoffs, and their proportion should therefore increase over time. On the contrary, for any proportion $q_2 > p^*$, the producers have higher fitness payoffs, and thus, p decreases. The only evolutionary stable strategy (ESS) is the proportion p^*. Any mutant trying to deviate from this proportion will be counter-selected, and the population comes back to the stable point (*solid circle*). The "group optimum" (in that order), which maximizes the individual payoffs, corresponds to a population of pure producers $p = 0$ (*open circle*), but it is an unstable optimum: a scrounger mutant would largely benefit from the producers' efficiency to locate food and will therefore quickly invade the population up to the ESS point

increases (Fig. 1). The optimal situation at the group level (group optimum) that would maximize the payoffs for all the individuals is thus a pure population of producers ($p = 0$, open circle in Fig. 1), but it is not a stable state. Indeed, an individual which begins to play as a scrounger largely benefits from its rare behavior, and its expected fitness payoffs are much larger than those of the producers. Consequently, it will have a greater probability of contributing to the next generation, and its behavior quickly spreads in the population. The proportion of scroungers increases up to p^* (solid circle in Fig. 1) which is the ESS: any deviation from this proportion would be counter-selected. A remarkable feature of such a game is that the ESS (Fig. 1; solid circle) leads to much higher payoffs than the population optimal strategy (Fig. 1; open circle). Evolution does not necessarily comply with the general interest. This idea is very similar to the "tragedy of the commons" in economy (Hardin 1968).

Future Directions

Since the seminal book by John Maynard Smith (1982), the concept of ESS is not only considered as a central concept in evolutionary biology, but it also attracted the attention of economists (Hammerstein and Hagen 2005; Weibull 1997). The field of evolutionary game theory has developed in many directions. The analysis described above essentially focused on the ESS because it is easier to analyze the equilibrium than the dynamical trajectories leading to the equilibrium. Yet, the ESS is essentially a question of stability around the equilibrium point: the population can both resist the invasion by mutants and move back to the ESS after a perturbation. But the definition of ESS does not guarantee that any potential ESS can evolve in the first place, i.e., when it is the rare mutant itself. The background environment might not be favorable enough to ensure its initial spread. This particular question is specifically addressed by the field of *adaptive dynamics (*Diekmann 2004*;* Waxman and Gavrilets 2005).

Another important concern about the concept of ESS is related to its heuristic value in animal behavior. Evolutionary game theory essentially aims at proposing normative models about the outcome of complex interactions between agents and the resulting equilibrium strategy, with limited assumption about the underlying decision-making processes. It is a powerful mechanism to describe the evolution of phenotypes across generation, allowing the application of game theory analysis to any living organisms, regardless of their cognitive abilities, as long as they are submitted to the evolutionary processes of replication, mutation, and selection. It is a convenient way to escape the demanding assumption of classical game theory about the players' capacity to understand the rules of the interactions and to think rationally. It is however important to note that the evolutionary time scale is measured in a number of generations. In other words, the convergence toward the ESS is based on the very slow process of selection of the most efficient strategies across generations. This mechanism is not relevant for most behaviors of interest. The animals constantly make short-term adjustments of their behaviors in response to changes in the social context. These adjustments can occur through learning, reinforcement, trials and errors, copying, or cultural transmission. Superficially, these mechanisms appear consistent with the fundamental mechanisms at the very basis of the evolutionary game theory: if a new behavior (mutation) performs well (selection), it could be adopted by other members of the population (replication). But they also assume advance cognitive skills such as memory, ability to compare the frequency-dependent payoffs, learning, and behavioral flexibility. The apparently simple ecological mechanisms invoked in the definition of the ESS had led many behavioral ecologists to disregard the question of the underlying decision-making process. At most, they assumed that the underlying cognitive machinery itself should evolve by natural selection in order to generate behaviors close to the ESS. It is still an open question whether the limited learning skills allow the convergence toward strategies close to the ESS (Fawcett et al. 2013; Hagen et al. 2012). Even if the concept of ESS has an enormous interest as a normative model, it might be of very limited interest as a descriptive model because it fails to encapsulate the underlying processes of decision-making. Hopefully, these mechanism are currently the object of a growing interest in behavioral ecology (Fawcett et al. 2014), and this research could, in turn, spawn new development in game theory.

References

Dechaume-Moncharmont, F.-X., Brom, T., & Cézilly, F. (2016). Opportunity costs resulting from scramble competition within the choosy sex severely impair mate choosiness. *Animal Behaviour, 114*, 249–260. https://doi.org/10.1016/j.anbehav.2016.02.019.

Diekmann, O. (2004). A beginners guide to adaptive dynamics. *Banach Center Publications, 63*, 47–86. Retrieved from http://igitur-archive.library.uu.nl/math/2006-0727-200409/UUindex.html.

Fawcett, T. W., Fallenstein, B., Higginson, A. D., Houston, A. I., Mallpress, D. E. W., Trimmer, P. C., & McNamara, J. M. (2014). The evolution of decision rules in complex environments. *Trends in Cognitive Sciences, 18*(3), 153–161. https://doi.org/10.1016/j.tics.2013.12.012.

Fawcett, T. W., Hamblin, S., & Giraldeau, L.-A. (2013). Exposing the behavioral gambit: The evolution of learning and decision rules. *Behavioral Ecology, 24*(1), 2–11. https://doi.org/10.1093/beheco/ars085.

Frey, E. (2010). Evolutionary game theory: Theoretical concepts and applications to microbial communities.

Physica A: Statistical Mechanics and its Applications, 389(20), 4265–4298. https://doi.org/10.1016/j.physa.2010.02.047.

Giraldeau, L.-A., & Caraco, T. (2000). *Social foraging theory*. Princeton University Press. Retrieved from http://www.worldcat.org/isbn/0691048762.

Hagen, E. H., Chater, N., Gallistel, C. R., Houston, A., Kacelnik, A., Kalenscher, T., … Stephens, D. W. (2012). Decision making: What can evolution do for us? In P. Hammerstein & J. R. Stevens (Eds.), *Evolution and the mechanisms of decision making* (pp. 97–126). Cambridge, MA: The MIT Press.

Hammerstein, P., & Hagen, E. (2005). The second wave of evolutionary economics in biology. *Trends in Ecology & Evolution, 20*(11), 604–609. https://doi.org/10.1016/j.tree.2005.07.012.

Hardin, G. (1968). The tragedy of the commons. *Science, 162*(3859), 1243–1248. https://doi.org/10.1126/science.162.3859.1243.

Hori, M. (1993). Frequency-dependent natural selection in the handedness of scale-eating cichlid fish. *Science, 260*(5105), 216–219. https://doi.org/10.1126/science.260.5105.216.

Llaurens, V., Raymond, M., & Faurie, C. (2009). Why are some people left-handed? An evolutionary perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1519), 881–894. https://doi.org/10.1098/rstb.2008.0235.

Maynard Smith, J. & Price, G. R. (1973). The logic of animal conflict. *Nature 246*, 15–18. https://doi.org/10.1038/246015a0.

Maynard Smith, J. (1982). *Evolution and the theory of games*. Cambridge: Cambridge University Press.

Nash, J. F. (1950). Equilibrium points in N-person games. *Proceedings of the National Academy of Sciences, 36*(1), 48–49. https://doi.org/10.1073/pnas.36.1.48.

von Neumann, J., & Morgenstern, O. (1944). *Theory of games and economic behavior*. Princeton: Princeton University Press. Retrieved from http://www.worldcat.org/isbn/0691130612.

Waxman, D., & Gavrilets, S. (2005). 20 questions on adaptive dynamics. *Journal of Evolutionary Biology, 18*(5), 1139–1154. https://doi.org/10.1111/j.1420-9101.2005.00948.x.

Weibull, J. W. (1997). *Evolutionary game theory*. Cambridge: MIT press.